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The *Oniscus asellus* complex (Crustacea: Isopoda: Oniscidea) in the Iberian Peninsula with the description of a new species

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The *Oniscus asellus* complex (Crustacea: Isopoda: Oniscidea) in the Iberian Peninsula with the description of a new species. - Extensive fieldwork in the northwest of the Iberian peninsula has resulted in the discovery of *Oniscus galicianus* sp. nov. which is closely related to *ancarensis* Bilton, and *asellus* Linnaeus. Together these three taxa are considered to form a distinct clade within the genus-the *asellus* complex. *O. galicianus* is described and distinguished from other members of the complex using pleopodal anatomy and multivariate morphometry. The discovery of *galicianus* significantly modifies previous ideas concerning the distribution and evolution of the *asellus* complex in southwest Europe. Only the nominate subspecies of *O. asellus* occurs in the Iberian peninsula. This finding is discussed and the suggestion made that the intraspecific taxa of *asellus* differentiated elsewhere in western Europe.

Key-words: woodlouse - systematics - Spain - biogeography - new species.

INTRODUCTION

The genus *Oniscus* was revised by Bilton (1992) who recognised four species, three of which are confined to the extreme south-west of Europe. Subsequent to this it was discovered that *Oniscus asellus* Linnaeus consists of two subspecies and a multitude of intermediate populations which appear to be of hybrid origin (Bilton 1994). In 1990 a population of *Oniscus* was sampled in the province of La Coruña, Galicia, northern Spain and identified as belonging to *O. asellus* s. lat. These animals were included as intermediates between *asellus* and *occidentalis* Bilton (Bilton 1994). The author conducted further extensive fieldwork in the northwest of the Iberian peninsula during the first half of 1993, when a number of similar populations of *Oniscus* were discovered. A thorough consideration of the morphology and ecology of these isopods has led to the conclusion that rather than belonging to *asellus* these represent yet another endemic species of the genus. This is described here, along with a discussion of the occurrence of the *asellus* complex in the northwest of the peninsula.

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MATERIALS AND METHODS

Specimens referred to in this study were collected by hand searching in a number of localities in northwest Spain. Speciemens were collected into 70% ethanol in which they are stored. Type material is deposited in a number of institutions which are referred to in the text with the following abbreviations:

DTB Coll. D.T. Bilton, Plymouth.
MHNG Muséum d'Histoire naturelle, Genève.
MZUF Museo Zoologio dell'Università, Firenze.
NHML Natural History Museum, London.
USC University of Santiago de Compostela, Dept. of Biology.

In order to test the reliability of these characters in separating *galicianus* from *asellus* specimens of both species from various localities (Table 1) were scored for the following measurements: total body length, maximum width of pereonite 4, length of lateral lobe, width of lateral lobe at base, length of telson, width of telson projection at base, and width of "respiratory region" on the exopodite of pleopod 1 (Fig. 1). A canonical discriminant functions analysis (Reyment, Blackith & Campbell 1984) was performed on measurements taken, using SPSS 4.0 on a Macintosh LC630 computer, with four groups defined corresponding to the two sexes of the two species.

Table I

Specimens of *Oniscus galicianus* sp. nov. and *O. asellus asellus* included in the statistical analysis.

Taxon	Locality	♂♂	♀♀
Oniscus galicianus sp. nov.	SPAIN, Lugo, Rio Pambre	1	
	SPAIN, Lugo, Montes de Valcaloura	1	4
	SPAIN, Lugo, Vilar de Donas	6	
	SPAIN, Lugo, Rio Ferreira	2	3
	SPAIN, Lugo, S. of Meira	1	
	SPAIN, Lugo, Rio Xudan	2	3
	SPAIN, Lugo, Rio Landro	2	2
	SPAIN, Coruña, A Capela Caaveiro	1	
Oniscus asellus asellus	SPAIN, Coruña A Capela Caaveiro	7	
	SPAIN, Asturias, Sierra de los Vientos	2	1
	SPAIN, Pontevedra, Carboeiro	2	2
	SPAIN, Lugo, Baralla	1	
	SPAIN, Lugo, Rio Fereirra	1	2
	SPAIN, Lugo, Vilar de Donas	1	2
	MADEIRA, Fajã Grande de Ca.	1	
	SCOTLAND, Fair Isle	2	
	ENGLAND, Durham, Witten Park	4	

TAXONOMY

Oniscus galicianus sp. nov.

Material examined

Spain. Galicia: 1♂ Holotype, Prov. La Coruña, A Capela Caaveiro. Atlantic *Quercus/Castanea* wood along Rio Eume NE of Pontedeume. D.T. Bilton leg. 6/II/1993. (MZUF). 1♀ paratype, same loc. D.T. Bilton leg. 13/II/1993. (USC). 1♀ paratype, Prov. Lugo, beside Rio Pambre along N547 road, small area of *Quercus* by river. D.T. Bilton leg. 7/II/1993. (DTB). 6♀♀ paratypes, Prov. Lugo, beside Rio Ferreira close to Vilar de Donas along N547 road, small *Quercus* grove beside water. D.T. Bilton leg. 7/II/1993. (2♀♀ MZUF, 4♀♀ DTB). 2♂♂, 3♀♀ paratypes, Prov. Lugo, along Rio Ferreira close to N547-N540 road junction, small grove of *Betula*, *Quercus* and *Castanea* on riverbank. D.T. Bilton leg. 11/II/1993. (1♂, 1♀ MZUF, 1♂, 2♀♀ USC). 3♂♂, 6♀♀ paratypes, Prov. Lugo, E of Palas de Rei, beside N547 road, *Quercus* grove by small stream. D.T. Bilton leg. 11/II/1993. (DTB). 1♂, 4♀♀ paratypes, Prov. Lugo, Montes de Valcaloura 3 km N of Taboada along N540 road, Quercus grove along tiny stream. D.T. Bilton leg. 20/II/1993. (1♂, 1♀ NHML, 3♀♀ DTB). 2♂♂, 3♀♀ paratypes Prov. Lugo, gorge along Rio Xudan NE of Meira, *Quercus* wood with *Saxifraga* and seeps beside stream. D.T. Bilton leg. 21/II/1993. (MHNG). 1♀ paratype, Prov. Lugo, S of Meira along N640 road, *Quercus* grove. D.T. Bilton leg. 21/II/1993. (USC). 3♂♂, 4♀♀ paratypes, 2♀♀ juveniles, Prov. Lugo, 10 km E of Vilar de Donas, *Quercus* grove beside Rio Ferreira along N547 road. D.T. Bilton leg. 14/v/1993. (DTB). 3♂♂, 2♀♀ paratypes, 9♂♂, 12♀♀ specimens, Prov. Lugo, Xerdiz, *Quercus/Castanea* grove beside Rio Landro, under *Rubus* litter and grasses on damp sandy soil. D.T. Bilton leg. 15/v/1990. (Paratypes MZUF, other specimens DTB).

Description

Body (Fig. 2) an elongate flat oval, somewhat parallel-sided over the middle of the pereon. Length 8.8 mm (7.0-13.6 mm in paratypes) maximum width, at pereonite 4, 4-9 mm (3.4 -6.9 in paratypes). Dorsal surface smooth and covered in small triangular tricorns (Holditch 1984) spaced roughly a spine's width apart. Cephalon (from above) twice as broad as long with weak dorsal tuberculation, especially close to the front margins and around the eyes. Frontal lobe obtusely triangular and pointed as in similarly sized *O. asellus*. Lateral lobes shorter than in asellus, almost square-shaped with bluntly-rounded apices. Frontal line as in *asellus*. Eyes each of 18 ocelli. Pereonites 1-3 with posterior borders strongly sinuate at the sides, pereonites 4-7 with posterior borders much more strongly sinuate, sinuation occupying at least the outer two-thirds of segments 4-6 and the entire posterior margin of segment 7. Pereon epimera quite narrow; when viewed from below taking up less than half the total width at segment 4. Apices of epimera sharply pointed,becoming more acuminate on moving down the body. Pleon epimera on segments 3-5 strongly curved and sharply pointed. Telson with a bluntly-pointed projection whose width is half the length of the segment. Telson projection much broader and more rounded than that of *O. asellus*. Uropodal exopod extending beyond the telson by a further projection's length. Last segment of exopod an evenly-curved elongate pointed cylinder slightly flattened dorsoventrally and with a flat outer ventolateral face. Dorsal surface of animal without tuberculation except that surrounding the pale

muscle-attachment sites on the pereon, this being particularly marked on the anterior three segments. Colour in alcohol light brownish grey with paler mottling. Cephalon brownish with symmetrically arranged paler spots. Each pereonite with grey-brown base pigment broken by a characteristic pattern of paler areas. Pereonites lacking the greenish yellow areas of "fatty tissue" noted in asellus (BILTON 1994). The pereon is bisected by a pale line above the gut, to each side of which there are a series of longitudinal pale streaks and blotches probably representing areas of muscle attachment. These are more extensive than in typical *asellus asellus*, and resemble the state of development seen in *asellus occidentalis*. These areas are flanked by another pigmented area broken by a pale streak representing the attachment area of the pereopods. Outside this the epimera are again brownish grey, but slightly paler than the rest of the body. The pleon is uniformly brownish grey marked with paler patches each side of the mid-line up to segment 4. In life the colour appears slightly more blue-grey, the animal having a somewhat translucent appearance, and the epimera are often marked with orange- brown spots at their apices. Exopodite of first pleopod characteristic in both sexes (Fig. 1). Shape similar to that of *asellus*, but the outer "respiratory region" (VANDEL 1962) much narrower than in this species, always under 0.3 mm wide.

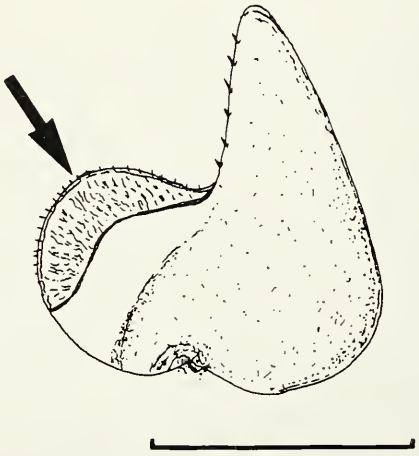


FIG. 1

Oniscus galicianus sp. nov., SPAIN, Lugo, Rio Ferreira. Female first pleopodal exopodite. Arrow indicates area where width of the "respiratory region" was calculated. Scale bar 1 mm.

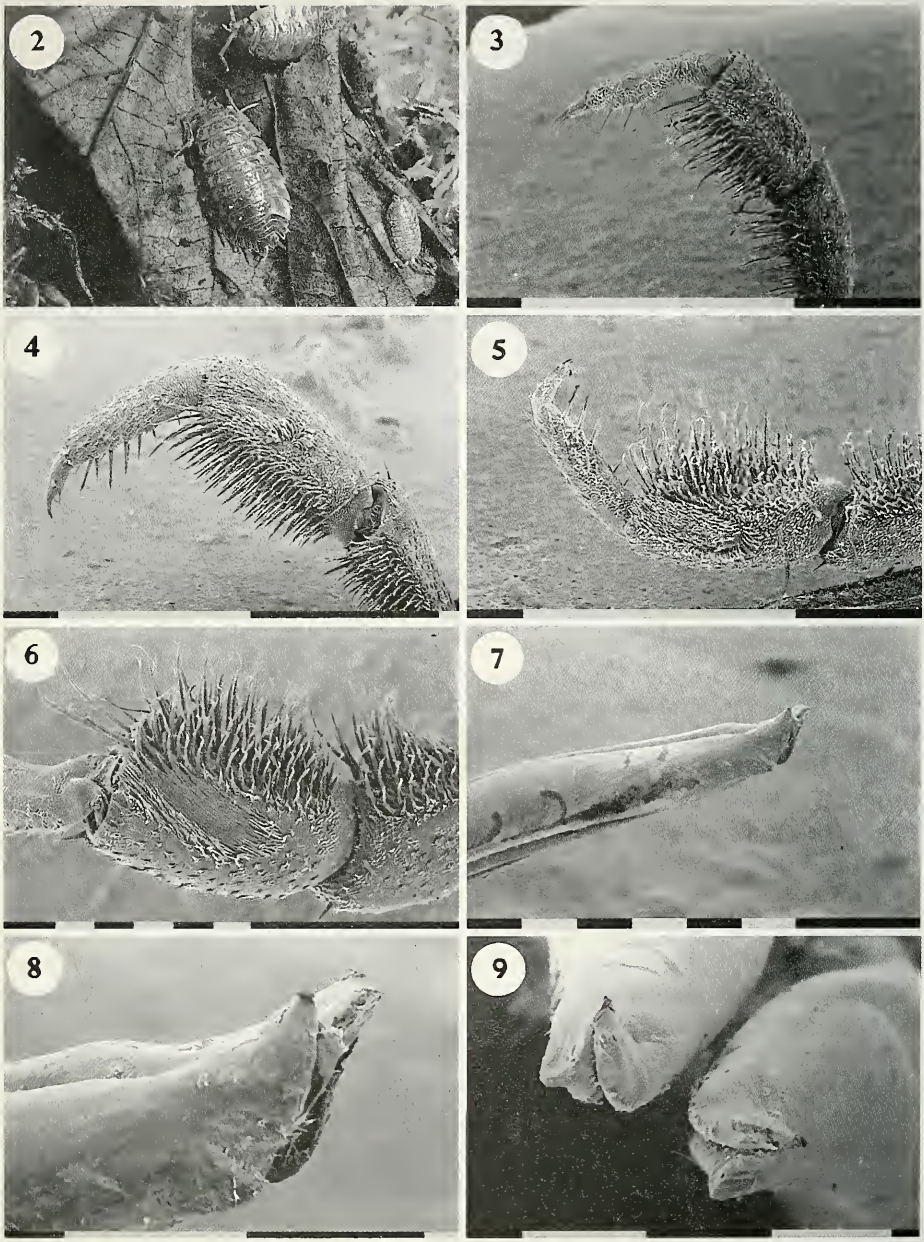
Male

Pereopod 1 with long, somewhat curved spines on the underside of the merus and carpus (Fig. 3). These spines are longer than in *asellus asellus* (Fig. 4) and are of markedly uneven length. The spines appear straighter and less dense than those of *asellus occidentalis* (Fig. 5) or intermediate *asellus* populations (Fig. 6). Carpus with plumose setae on inner face as in asellus s. lat. Endopodite of pleopod 1 appearing swollen dorsally towards the apex (Figs 7 & 8), superficially similar to some individuals of *asellus* s. lat. When seen in apical view (Figs. 9 & 10) the endopodite apex is clearly different to that of any known *asellus* (Figs 11-13). The swelling in *galicianus* is formed by an evenly curved outer dorsolateral ridge, not a more localised bump or projection. This ridge is also clearly distinct from the lateral projection seen in *O. ancarensis* (Fig. 14) from the extreme West of the Cordillera Cantabrica (BILTON 1992).

Recognition of the new species

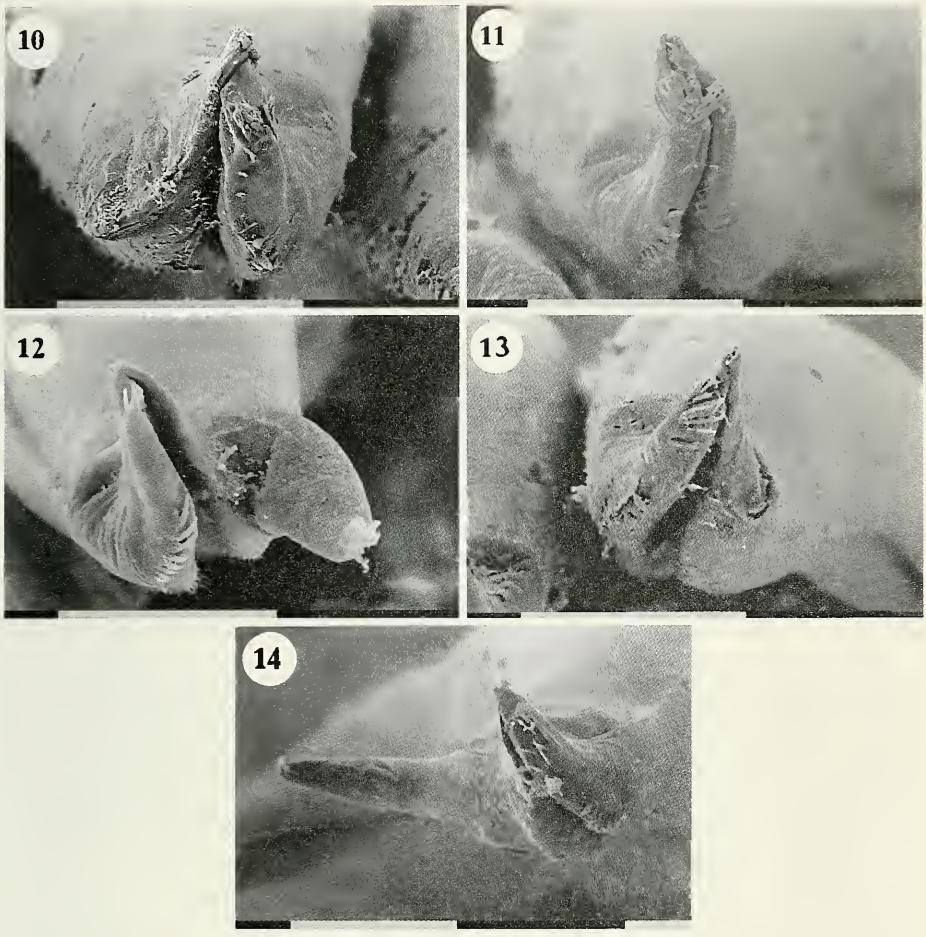
Oniscus galicianus is sympatric with *Oniscus asellus asellus* (sensu BILTON 1994) and *Oniscus lusitanus* Verhoeff. Only *asellus* has been taken in the same sites as *galicianus*, and the two have been found to occupy quite different microhabitats (see below), a fact which first suggested the existence of independent taxa. The new species would key to *Oniscus asellus* in BILTON (1992). The most reliable character for distinguishing *galicianus* from populations of *asellus*, both in Iberia and elsewhere is the width of the "respiratory region" of the first pleopodal exopodite of both sexes. As described this is relatively narrow in the new species, widths of 0.10 - 0.30 ($X = \bar{0.16}$) mm being recorded amongst the type series. The width of this area was 0.2 - 0.7 ($X = \bar{0.39}$) mm in the sample of *asellus asellus* examined (see below) which included individuals from Iberia and across the species' range. A two-tailed t-test (SOKAL & ROLF 1995) indicated that the means of this character are significantly different ($P<0.01$) between the samples of the two species. In addition to the pleopodal exopod, *galicianus* can be distinguished on a number of features. The species can be separated from *O. asellus asellus* by its narrower pereon and shorter and broader frontal lobes and telson. Males can be further recognised by the structure of the apex of the first pleopodal endopodite (Figs 7-10) and the structure of the first pereopods (Fig 3), characters which also allow *galicianus* to be separated from *O. asellus occidentalis* and intermediate *asellus* populations *sensu* BILTON (1994).

In the discriminant functions analysis almost all the variance was explained by the first two discriminant functions which accounted for 72.5 and 24.8% of the total variance respectively. Pooled within-group correlations between measured variables and the discriminant functions are shown in table 2. From the table it is clear that the first discriminant function is mainly a function of "respiratory region" and telson width, whilst the second describes body and lateral lobe shape. The group to which an individual would be predicted to belong based on its discriminant score was compared with its actual group (SPSS, 1983) for each specimen in the analysis, and the results of this reclassification are summarized in table 3. It is immediately evident



FIGS 2-9

2. *Oniscus galicianus* sp. nov., SPAIN, Lugo, Rio Landro at Xerdiz. Living individual 10mm in length; 3. *Oniscus galicianus* sp. nov., SPAIN, Lugo. Rio Landro. Male first pereopod, internal face. Scale bar 1 mm.; 4. *Oniscus asellus asellus*, ENGLAND, Carlisle, Beechgrove. Male first preopod, internal face. Scale bar 1 mm.; 5. *Oniscus asellus occidentalis*, JERSEY, Greve de



FIGS 10-14

10. *Oniscus galicianus* sp. nov., SPAIN, Lugo, Rio Landro. Male fist pleopodal endopodites, apical view. Close-up of right pleopod. Scale bar 0.1 mm.; 11. *Oniscus asellus asellus*, ENGLAND, Carlisle, Beechgrove. Endopodite of male left first pleopod, apical view. Scale bar 0.1 mm.; 12. *Oniscus asellus occidentalis*, ENGLAND, Devon, Lydford Gorge. Endopodite of male left first pleopod, apical view. Scale bar 0.1 mm.; 13. *Oniscus asellus* intermediate, ENGLAND, Yorks, Stony Ciffe Wood, Netherton. Endopodite of male left first pleopod, apical view. Scale bar 0.1 mm.; 14. *Oniscus ancarensis*, SPAIN, Léon, N edge of Priaranza. Endopodite of male left first pleopod, apical view. Scale bar 0.1 mm.

Lecq. Male first pereopod, internal face. Scale bar 1 mm.; 6. *Oniscus asellus* intermediate, ENGLAND, Wychwood Forest. Male first pereopod, internal face. Scale bar 1mm.; 7. *Oniscus galicianus* sp. nov., SPAIN, Lugo, Rio Landro. Endopodites of male first pleopods, lateral view. Scale bar 0.1 mm.; 8. *Oniscus galicianus* sp. nov., SPAIN, Lugo, Rio Landro. Close-up of apices of male first pleopodal endopodites. Scale bar 0.1mm.; 9. *Oniscus galicianus* sp. nov., SPAIN, Lugo, Rio Landro. Male first pleopodal endopodites, apical view. Scale bar 0.1mm.

that all *asellus* individuals are correctly classified with this species, indeed only 9.5% of females being misclassified at all, as males of the same species. In the case of *galicianus* some individuals of both sexes could be misclassified with *asellus*, but in this taxon 83% of females and almost 94% of males would be correctly placed, indicating the value of the chosen characters in distinguishing the two taxa.

DISCUSSION

The description of *galicianus* increases the number of *Oniscus* species to five. All except the widespread European *O. asellus* s. lat. are restricted to the Iberian peninsula and adjacent southwest Europe. Three species, *ancarensis*, *lusitanus* and *galicianus* are endemic to the extreme west of the peninsula. *O. ancarensis* has been taken from the Sierra de Ancares and adjacent areas in the Galician west of the Cantabrian mountains, where it can be found sparingly in wet *Quercus* and *Castanea* woods (pers. obs.). From available information this species appears to be allopatric to all other *Oniscus*, not even *asellus* having been found in this area. It appears that *ancarensis* is endemic to the end of the Cantabrian chain, finds being restricted to Ancares, Serra do Courel and nearby regions on the Lugo-Léon border. *O. lusitanus* has a distribution ranging from central Portugal to Asturias (Bilton 1992; Schmilzer 1971). The species is most abundant in the extreme north of Portugal and the south of Galicia in Pontevedra province, and appears to be more thermophilous than other members of the genus. In the north and east of its range *lusitanus* becomes very scarce, and has not so far been taken in the colder region of central Lugo where most *galicianus* localities are situated. *O. galicianus* then co-occurs only with *O. asellus*. The ecology of these two species in the region is quite different however, and this is examined below along with a discussion of *O. asellus* in the northwest of Iberia.

Table 2

2. Pooled within-group correlations between measured variables and the first two discriminant functions. An asterisk (*) indicates a significant association at the 0.1 level. Variables are as follows: total body length (1), max. width of pereonite 4 (2), length of lateral lobe (3), width of lateral lobe (4), length of telson (5), width of telson projection at base (6), and width of "respiratory region" on first pleopodal exopodite (7).

	Discriminant function	
	1	2
Variable		
7	0.71461*	0.44691
5	0.54467*	0.37630
2	0.43243	0.72722*
3	0.38950	0.58136*
1	0.30154	0.51260*
6	0.38555	0.47206*
4	0.22917	0.22399

TABLE 3

Summary table of actual and predicted group membership (based on discriminant scores) for *galicianus* and *asellus* specimens measured in the analysis.

ACTUAL GROUP		NO. OF CASES	PREDICTED GROUP MEMBERSHIP 1	2	3	4
asellus ♂	1	21	19 90.5%	2 9.5%	0 0.0%	0 0.0%
asellus ♀	2	7	0 0.0%	7 100.0%	0 0.0%	0 0.0%
galicianus ♀	3	12	2 16.7%	0 0.0%	7 58.3%	3 25.0%
galicianus ♂	4	16	0 0.0%	1 6.2%	4 25.0%	11 68.8%

ECOLOGICAL SEPARATION OF *asellus* AND *galicianus*

Oniscus galicianus has so far been reported from 10 localities in central Galicia, in the provinces of La Coruña and Lugo. The species' distribution is centred on the medium altitude areas of central Lugo, around the town of Melide, extending north to the Rio Landro basin and west to the Eume valley. Despite exhaustive fieldwork in adjacent areas of Galicia, Léon, Asturias and northern Portugal *galicianus* has not been taken outside this small area, and genuinely appears to be restricted to this part of Galicia. In comparison with surrounding areas central Lugo experiences a harsher climate, with cold fog frequently enveloping the landscape for most of the day during Autumn and Winter.

Oniscus asellus has also been taken in this region, indeed the species co-occurred with *galicianus* at 60% of localities. Where the two woodlice were found together it was clear that they occupied quite separate microhabitats. *O. asellus* was found in microsites typical of this species throughout its range; below bark of fallen trees, and under dead logs. In contrast *galicianus* was never found associated with timber, being taken in leaf litter or amongst damp soil. All the microsites from which the species was collected were extremely wet, usually being immediately adjacent to flowing watercourses, or actually within small seepages. On one occasion specimens were collected under trickling water beside a small waterfall (A Capela Caaveiro). On two occasions *O. galicianus* was collected together with *Miktoniscus bisetosus* Vandel, 1946, a trichoniscid of saturated organic soil beside small streams. The reduced size of the "respiratory region" compared to *asellus* may be relevant here, since *galicianus* is tied to wetter microsites than other *Oniscus*, being almost amphibious.

Systematic placement of *galicianus* and the occurrence of the *asellus* complex in northwestern Iberia

It is clear that galicianus is very closely related to *asellus* and *ancarensis*. These three species appear to form a distinct clade within *Oniscus* (here referred to as the *asellus* complex), defined by a smooth dorsal surface in adults and (except in *O. asellus asellus*) a complex structure to the apices of the endopodites of the first male pleopods.

Whilst *ancarensis* and *galicianus* are localized endemic species restricted to the extreme northwest of Spain, *asellus* occurs widely in Europe and has been divided into two distinct subspecies (*asellus* and *occidentalis*) which appear to hybridise extensively (Bilton, 1994). As noted earlier previous records of hybrid individuals from Galicia, which led to the suggestion that both subspecies of *asellus* must be present in northern Iberia, are in fact referrable to *galicianus*. All *asellus* material seen from Spain and Portugal belongs to the widespread nominate subspecies. The nearest *occidentalis* appears to get to the Iberian peninsula is the French east Pyrenees (Bilton 1994). Given the extensive fieldwork conducted by the author in 1993 it appears likely that *occidentalis* is truly absent from Iberia. This absence is quite unexpected, and alters considerably hypotheses regarding the differentiation of *asellus* and *occidentalis*. Bilton (1994) considered that the taxa diverged in the Iberian peninsula as a result of climatic fluctuations and habitat shift during the Pleistocene. Such a scenario demands that *asellus* and *occidentalis* coexisted in Iberia during some time in the recent past, an idea which was supported by the supposed hybrid individuals from Galicia. Now it is clear that only *asellus* s.str. is found in Iberia it seems more likely that the split into two taxa occurred elsewhere, since there is no good climatic or ecological reason for the absence of *occidentalis* from the area. *O. a.occidentalis* is restricted to the British Isles and western France and assuming that its differentiation from *asellus* occurred as a result of isolation in separate refugia during Pleistocene climatic cycles such refugia could be postulated to have been situated in Southern France, an area known for its high diversity of endemic isopods which have apparently differentiated *in situ* (Vandel 1960; 1962). Under such a scenario Iberian populations of *asellus* could be seen as Postglacial invaders, rather than the source from which the species expanded in the Holocene. Genetic phylogeographical studies of extant populations of this complex will be invaluable if we are to understand its evolution and spread in Europe and the implications this may have to Pleistocene biogeography..

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